

ZOOPLANKTON AND LARVAL FISH COMMUNITY DEVELOPMENT: COMPARATIVE STUDY UNDER FIRST-YEAR SEA ICE AT LOW AND HIGH LATITUDES IN THE NORTHERN HEMISPHERE*

Louis FORTIER¹, Martin FORTIER¹ and Serge DEMERS^{2**}

¹GIROQ, Département de Biologie, Université Laval, Ste-Foy, Québec, Canada, G1K 7P4

²Institut Maurice-Lamontagne, Ministère des Pêches et des Océans,
P.O. Box 1000, Mont-Joli, Québec, Canada, G5H 3Z4

Abstract: We compared the development of the zooplankton community in relation to the ice-algal bloom in Saroma Ko lagoon and Resolute Passage in spring. In Saroma Ko, mysids and copepods were the dominant components of the zooplankton. Numerically, *Pseudocalanus* spp. represented more than 73% of the copepod assemblage. The constancy of *Pseudocalanus* stage composition and the low production of copepod eggs and nauplii indicated that ice algae in the lagoon did not stimulate the development of copepods in spring. During the sampling period, the colonization of Saroma Ko by the larvae of several species of marine fish coincided with low production of zooplankton prey in the lagoon. In Resolute Passage, the hyperiid amphipod *Themisto libellula* and the copepod *Pseudocalanus acuspes* dominated the zooplankton. The population of *Pseudocalanus acuspes* (78% of the copepod assemblage) evolved from a majority of overwintering CIV and CV copepodites in early May to a majority of females in late June. The production of eggs and nauplii increased over this period and started well before the massive release of ice algae or the phytoplankton bloom. This suggests that *Pseudocalanus acuspes* reproduction may be fuelled by endogenous reserves from the previous fall and/or the grazing of ice algae falling from the ice-cover. Few fish larvae were sampled in Resolute Passage, indicating that this area of strong advection is probably unsuitable for the reproduction of fish. Our results for Saroma Ko lagoon and Resolute Passage support the hypothesis that, in seasonally ice-covered seas, the importance of the ice-algal cycle to the maturation of *Pseudocalanus* increases with latitude.

1. Introduction

In seasonally ice-covered Arctic and subarctic seas, some larvae of winter spawning fishes are transported in coastal areas still covered with ice (DROLET *et al.*, 1991; GILBERT *et al.*, 1992; FORTIER *et al.*, 1995). In these seas, the growth and reproduction of some grazers depend on two distinct production cycles: the bloom of ice-algae in bottom ice and at the ice-water interface, and the phytoplankton

* Contribution to the research programs of GIROQ (Groupe interuniversitaire de recherches océanographiques du Québec) and Institut Maurice-Lamontagne (Ministère des Pêches et des Océans).

** Present address: Centre Océanographique de Rimouski, INRS-Océanologie, 310 Allée des Ursulines, Rimouski, Québec, Canada, G5L 3A1.

bloom in the water column after the ice break-up (HORNER, 1985; LEGENDRE *et al.*, 1992; HORNER *et al.*, 1992). The development of microalgae at the ice-water interface triggers the early growth and reproduction of copepods before the summer phytoplankton bloom (BEDO *et al.*, 1990; CONOVER *et al.*, 1988, 1991; CONOVER and HUNTLEY, 1991; RUNGE and INGRAM, 1988, 1991; RUNGE *et al.*, 1991; DROLET *et al.*, 1991; GILBERT *et al.*, 1992; FORTIER, 1994). Copepod eggs and nauplii then become available for first-feeding fish larvae several weeks before this phytoplankton bloom (DROLET *et al.*, 1991; RUNGE *et al.*, 1991; GILBERT *et al.*, 1992; FORTIER, 1994; FORTIER *et al.*, 1995).

Saroma Ko lagoon (northern Hokkaido, Japan) and Resolute Passage (North West Territories, Canadian Arctic) are respectively the southernmost and northernmost seasonally ice-covered areas in the Northern Hemisphere (Fig. 1). Resolute Passage is covered with ice for 9 months and longer, whereas Saroma Ko lagoon and the adjacent Sea of Okhotsk are rarely covered with ice for more than 4 months (TAGUCHI and TAKAHASHI, 1993). Accordingly, the relative duration and intensity of the ice-algal and phytoplankton production cycles differ widely between the two regions (DEMERS *et al.*, 1995). These differences are expected to affect the reproductive strategies of copepod grazers exploiting both cycles of production as well as the reproduction strategies of winter spawning fishes.

Based on the relative duration of the ice cover and of the summer phytoplankton cycle, it can be predicted that the importance of ice algal production for zooplankton development and larval fish first-feeding will be maximum in Resolute Passage and minimum in Saroma Ko lagoon. In this study, we tested this prediction by monitoring the production of fish larvae in relation to the production of ice algae

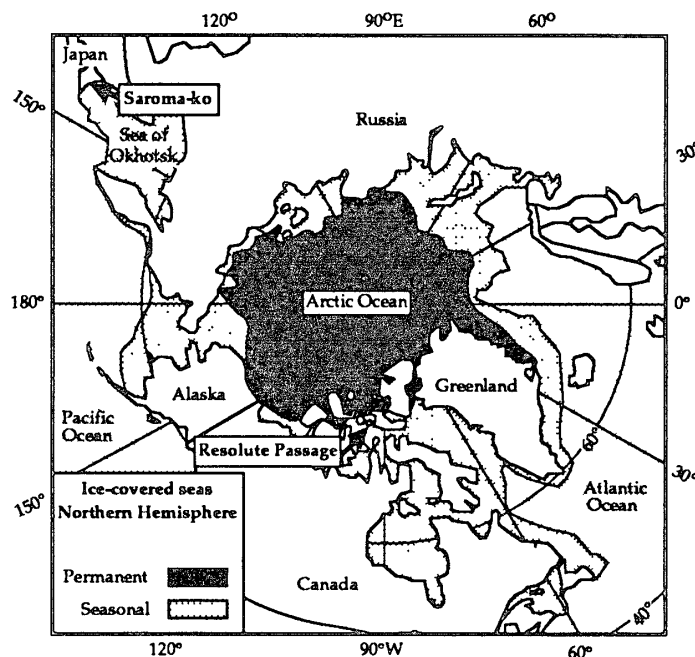


Fig. 1. Map of ice-covered seas in the Northern Hemisphere with location of Saroma Ko lagoon and Resolute Passage.

and the maturation of copepods under the ice cover of Saroma Ko lagoon and Resolute Passage.

2. Areas Studied and Methods

Saroma Ko lagoon ($44^{\circ}10'N$, $143^{\circ}45'E$) is the southernmost locale where sea ice forms in the Northern Hemisphere (Fig 1). The shallow (< 20 m) lagoon opens on the Sea of Okhotsk through two narrow inlets. Circulation is weak in the lagoon except in the immediate vicinity of the inlets. In normal years, the 30–40 cm thick ice cover is present on the lagoon from December to late March and, hence, light should not limit phytoplankton growth from April to December. At 30–40 cm in thickness, the ice cover may be thin enough to allow light to penetrate and phytoplankton to grow during the winter as well.

The density of ice algae and phytoplankton, and the stage composition of copepods were monitored at a single station in the lagoon from 21 February to 23 March 1992. Zooplankton was sampled under the ice with a pair of 50-cm diameter plankton nets (100 and $330\mu\text{m}$ meshes respectively) mounted on a bongo-type frame. The sampler was attached to a cable forming a loop between two holes 150 m apart in the ice, and was towed horizontally by a heavy-duty snowmobile (DROLET *et al.*, 1991). Circular buoys mounted on the frame allowed us to sample the layer immediately under the ice (FORTIER, 1994). Vertical profiles of salinity and temperature were recorded with a Seabird-19 CTD probe. Recruitment of fish larvae from the Sea of Okhotsk was monitored at the northeast inlet linking the lagoon to the Sea of Okhotsk from 28 February to 19 March 1992. Fish larvae entering or exiting the lagoon were sampled with a 50-cm diameter standard net ($500\mu\text{m}$ mesh) deployed from a bridge crossing the inlet, making use of tidal currents as the filtration force.

Resolute Passage ($74^{\circ}41'N$, $95^{\circ}16'W$) is among the northernmost areas in the Northern Hemisphere where the sea ice cover melts in summer (Fig. 1). The ice cover (*ca.* 2 m thick) starts forming in September and breaks up at the beginning of July. Tides and net circulation are strong in the Passage. The sun does not rise above the horizon from November to February. The short season of biological production starts in April with the development of ice algae that are released in the water column just before the ice break-up in early July. The break-up is followed by an intense phytoplankton bloom.

Ice algal and phytoplankton densities, copepod stage composition and fish larvae were monitored at a single site in the Passage from 7 May to 26 June 1992. A pair of 1-m^2 Tucker nets with $500\mu\text{m}$ mesh were deployed under the ice (using the same approach as in Saroma Ko) to collect macrozooplankton and fish larvae immediately under the ice cover. A 50-cm diameter standard net ($64\mu\text{m}$ mesh) was towed vertically from bottom to surface to sample zooplankton. Vertical profiles of salinity and temperature were recorded with a Seabird-19 CTD probe.

3. Results

3.1. Hydrography

Saroma Ko lagoon remained covered with ice during the entire sampling period. Snow thickness and hydrographic conditions varied little until mid-March when increasing air temperature reduced the snow cover and increased the input of freshwater in the surface layer immediately under the ice (Fig. 2). The complete ice breakup in the lagoon occurred during the first week of April. A small temperature gradient (0.4°C) existed in the water column until the beginning of March. At the end of March, water column temperature was more homogeneous vertically, at around -0.8°C . Before the melting of the ice cover in late March, salinity increased with depth from 29 to 31‰ in the top 2 m of the water column (Fig. 2). Below 2 m, salinity remained relatively constant with depth ($31\text{--}32\text{‰}$) throughout the study. Increased dilution ($24\text{--}29\text{‰}$) of the surface layer occurred with the melting of the ice cover in late March.

In Resolute Passage, temperature and salinity varied little vertically, with surface to bottom gradients of 0.2°C and 0.2‰ respectively. Some evidence of ice cover melting (surface salinities of 32.5‰) was detected after 24 June (Fig. 2).

3.2. Zooplankton assemblages

In Saroma Ko lagoon, copepods were the dominant component in numbers of the zooplankton assemblage sampled under the ice (Table 1). Among the copepods, *Pseudocalanus* spp. (73%), *Oithona* spp. (13%) and *Acartia* spp. (12%) were by far

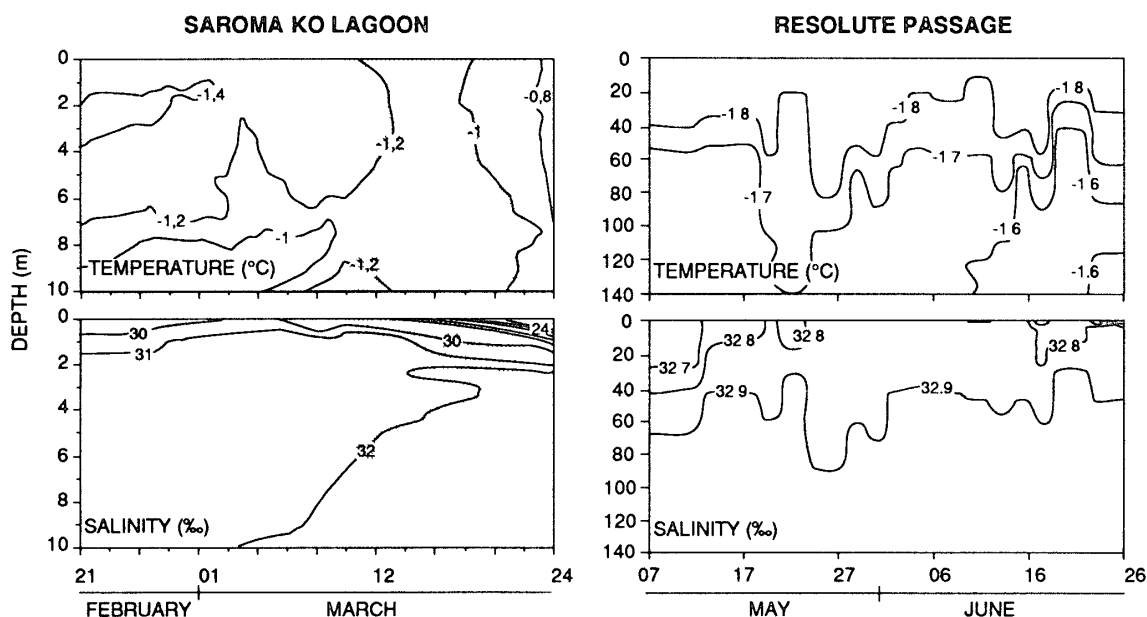


Fig. 2. Isotherms and isohalines under the ice of Saroma Ko lagoon (21 February to 24 March 1992) and Resolute Passage (7 May to 26 June 1992). Shaded area indicates interpolated data.

Table 1. Density of the major zooplankton taxa sampled in Saroma Ko lagoon (27 February to 21 March 1992) and Resolute Passage (7 May to 26 June 1992). Densities are given in $N m^{-3}$.

	Average density	Minimum density	Maximum density
Saroma Ko lagoon			
Mysidacea			
<i>Neomysis czerniawskii</i>	32	12	57
Copepoda			
<i>Pseudocalanus</i> spp.	757	238	1598
<i>Oithona</i> spp.	141	50	410
<i>Acartia</i> spp.	122	58	264
Nauplii	1875	820	4019
Resolute Passage			
Amphipoda			
<i>Themisto libellula</i>	12	0	70
Copepoda			
<i>Pseudocalanus acuspes</i>	488	52	1570
<i>Oncaea borealis</i>	40	0	80
<i>Oithona</i> sp.	37	7	80
<i>Calanus glacialis</i>	22	10	47
<i>Metridia longa</i>	10	6	25
<i>Calanus hyperboreus</i>	6	1	14
Nauplii	545	64	3895

the most abundant. The mysid *Neomysis czerniawskii* was abundant and surpassed the copepods in biomass.

Copepods were also the major contributors in numbers to the zooplankton assemblage of Resolute Passage. *Pseudocalanus acuspes* accounted for over 78% of the total in numbers. Macrozooplankton was dominated by the hyperiid amphipod *Themisto libellula* which could reach high concentrations ($>70 \text{ ind. m}^{-3}$) at night-time under the ice (Table 1).

3.3. Microalgal biomass, *Pseudocalanus* maturation and the production of larval fish prey

The accumulation of microalgal biomass immediately under the ice-water interface coincided with sporadic melt events, suggesting that melt water percolating through the ice cover washed ice microalgae into the top layer of the water column (Fig. 3). The taxonomic identification of water column microalgae confirmed this interpretation (C. MICHEL, Université Laval, personal commun). The final sedimentation of ice-algae around 16 March in Saroma Ko lagoon and around 25 June in Resolute Passage (Fig. 3b, f) coincided with the melt events that heralded the dislocation and final breakup of the ice cover (Fig. 2).

In Saroma Ko lagoon, the stage composition of the *Pseudocalanus* population remained remarkably stable over the sampling period, with a slight decrease in time in the proportion of females. All copepodite stages (CI through CV) were well represented (Fig. 3c). Densities of copepod nauplii in the water column were low

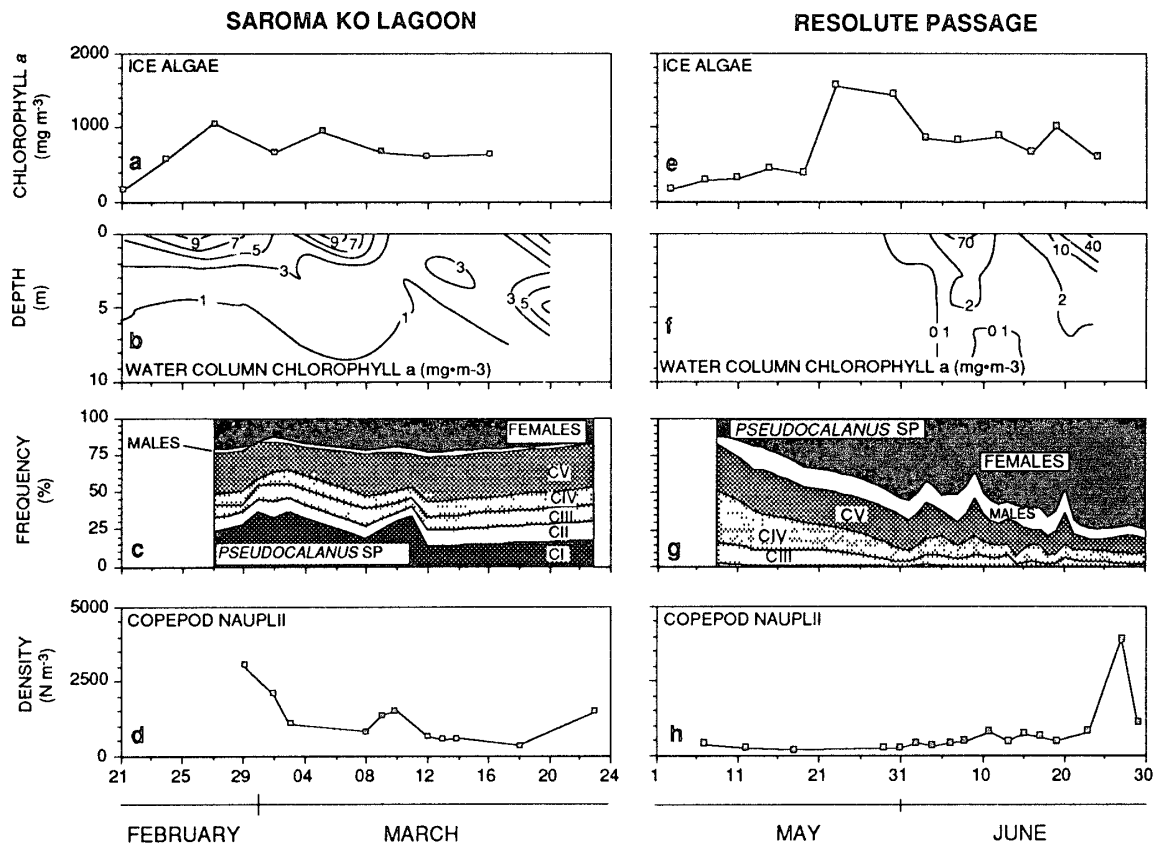


Fig. 3. Ice algae and water column microalgal biomass, stage composition of the dominant copepod *Pseudocalanus* sp. and density of copepod nauplii under the ice of Saroma Ko lagoon (21 February to 23 March 1992) and Resolute Passage (2 May to 28 June 1992).

throughout the study with an average of $1.2 \text{ nauplii L}^{-1}$ and a maximum of $3.5 \text{ nauplii L}^{-1}$ in late February (Fig. 3d).

In Resolute Passage, the development of the *Pseudocalanus* population was strongly pulsed, with the predominant overwintering stages (CIII to CV) in early May (85%) maturing quickly into females by late June ($>75\%$). Maturation into females started well before the massive release of ice algae from the ice, at a time when chlorophyll *a* concentration was $<0.1 \text{ mg m}^{-3}$ in the water column, suggesting that either internal reserves and/or direct grazing at the ice-water interface fuelled development (Fig. 3g). Densities of copepod nauplii in the water column were low. Nauplii became more abundant as the proportion of females increased in the copepod population (Fig. 3h).

3.4. Occurrence of fish larvae under the ice cover

In Saroma Ko lagoon, 1479 fish larvae belonging to 9 different species were caught at the inlet over the study period. Sand lance (*Ammodytes* sp.), snake prickleback (*Lumpenus sagitta*), sculpins (Cottidae) and walleye pollock (*Theragra chalcogramma*) made up the bulk of the assemblage (98.5%).

Sand lance larvae episodically entered the lagoon from the Sea of Okhotsk on

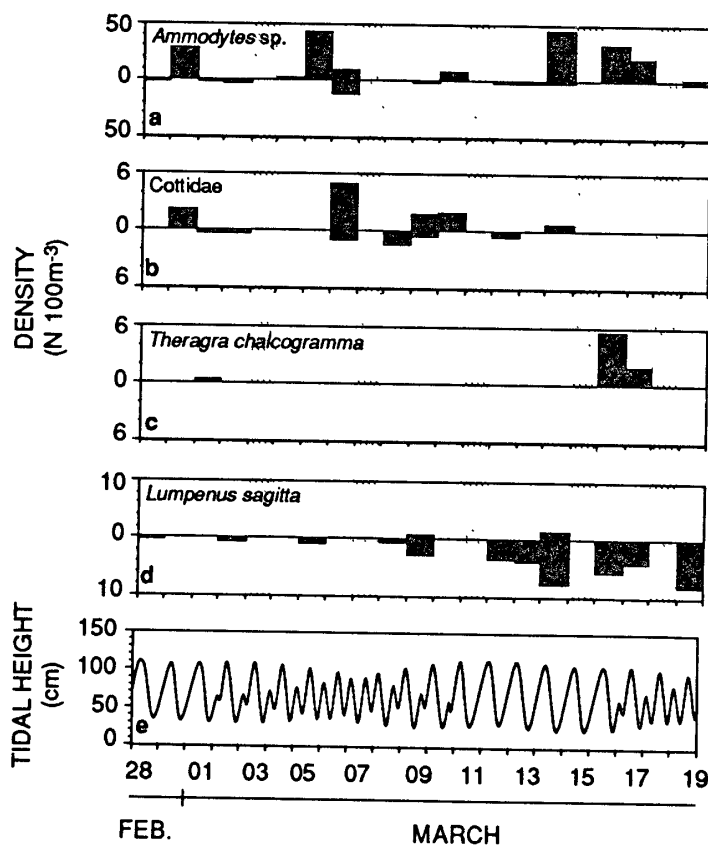


Fig. 4. Daily variation in the density of larvae of the dominant fish species captured at the inlet linking Saroma Ko lagoon to the Sea of Okhotsk from 27 February to 19 March 1992. Histograms of larval fish density during ebb are plotted upside down for contrast. Shaded areas indicate days with no data.

flood during the entire period (Fig. 4a). Sculpins recruited to the lagoon in early March primarily (Fig. 4b). Significant numbers of walleye pollock entered the lagoon on 16–17 March only (Fig. 4c). Finally, the number of snake prickleback larvae exiting the lagoon increased progressively from late February to the end of our sampling in late March (Fig. 4d). Recruitment of fish larvae into the lagoon did not appear related to the neap/spring cycle in tidal amplitude (Fig. 4e).

In Resolute passage, only 5 fish larvae and juveniles were caught under the ice during the sampling program. The larvae were all Arctic cod (*Boreogadus saida*).

4. Conclusions

In Resolute Passage, the maturation of the dominant copepod *Pseudocalanus acuspes* in the spring coincides with the production of ice algae. In these regions the season of phytoplankton production is short. The obvious advantage of exploiting the ice algae for maturation and reproduction is that the nauplii produced early will start feeding at the onset of the short phytoplankton bloom when food is plentiful. At these high latitudes, early reproduction is probably mandatory for *Pseudocalanus* to complete its life cycle within the year. Few fish larvae were captured in Resolute

Passage, suggesting that little fish reproduction took place in the area or at the time sampled.

In Saroma Ko, the stage composition of *Pseudocalanus* spp. remained remarkably constant during the period of release of ice-algae in the water column. Two interpretations are possible: either the populations did not develop at all at the sub-zero temperatures prevailing under the ice cover, or reproduction was continuous and slow, young stages replacing older ones at a constant rate. The presence of nauplii and *Pseudocalanus* CI and CII supports the second interpretation and suggests that *Pseudocalanus* was reproducing in the fall and during the winter months. In any case, the grazing of ice-algae in the top layer of the water column obviously had limited impact on the maturation rate and stage composition of *Pseudocalanus*. Given the high productivity of the lagoon and the warm temperatures prevailing in summer (up to 20°C), relatively small copepods such as *Pseudocalanus* have no difficulty producing more than one generation during the 8 months of ice-free conditions. Exploiting the ice-algal bloom would then provide these copepods with little advantage towards completing their life cycle. We conclude that, contrary to the populations of Arctic and subarctic seas such as Resolute Passage (this study) or Hudson Bay (RUNGE *et al.*, 1991), the maturation of overwintering *Pseudocalanus* in Saroma Ko lagoon depends little on the exploitation of ice algae.

Accordingly, the standing stock of copepod nauplii in Saroma Ko lagoon in winter was low. Since fish larvae feed almost exclusively on copepod nauplii at the onset of exogenous feeding, feeding conditions for young fish larvae were particularly poor under the ice cover during the winter months. The larvae of sand lance, the only species recruiting to some extent into the lagoon at that time, are well adapted to survive starvation at low temperature, until they can exploit the increased number of their prey after the ice break-up (*e.g.* KITAGAWA and YAMASHITA, 1986). Thus, in the spring and summer months, the lagoon could serve as a nursery area for sand lance larvae entering it before and after the ice breakup. This is in agreement with the suggestion by KITAGAWA and YAMASHITA (1986) that coastal embayments with a low degree of opening on the sea are important for the survival and growth of Japanese sand lance larvae (*Ammodytes personatus*) produced in the coastal zone.

Acknowledgments

This study was part of the Saroma-Resolute Study (SARES), a joint Canada-Japan research program on the biological productivity of Arctic and subarctic seas. Canadian participants were funded primarily by the Japan Science and Technology FUND of the Department of External Affairs and Trade of Canada. Additional support for this project came from research grants from the Natural Sciences and Engineering Research Council of Canada and the Fonds FCAR of Québec to LF and GIROQ. Infrastructure and logistical support were provided by GIROQ, the Polar Continental Shelf Project of Canada, and the Saroma Aquaculture and Research Institute (Tokoro, Hokkaido). Special thanks to Drs. H. HATTORI and

H. SAITO for enlightening discussions.

References

- BEDO, A. W., HEAD, E. J. H., CONOVER, R. J., HORNE, E. P. W. and HARRIS, L. R. (1990): Physiological adaptations of an under-ice population of *Pseudocalanus* in Barrow Strait (N.W. T) to increasing food supply in spring. *Polar Biol.*, **10**, 561–570.
- CONOVER, R. J., BEDO, A. J., HERMAN, A. W., HEAD, E. J. H., HARRIS, J. H. and HORNE, E. P. W. (1988): Never trust a copepod-some observations on their behavior in the Canadian Arctic. *Bull. Mar. Sci.*, **43**, 650–662.
- CONOVER, R. J., HARRIS, L. R. and BEDO, A. W. (1991): Copepods in cold oligotrophic waters-How do they cope? *Proceedings of the Fourth International Conference on Copepoda*, ed. by S.-I. UYE *et al.* *Bull. Plankton Soc. Jpn. Spec. Vol.*, 177–199.
- CONOVER, R. J. and HUNTLEY, M. (1991): Copepods in ice-covered seas-Distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. *J. Mar. Syst.*, **2**, 1–41.
- DEMERS, S., MONFORT, P., LAURION, I., SIME-NGANDO, T., ROBINEAU, B. and FORTIER, L. (1995): The microbial food web: Comparative study under first-year ice at low and high latitudes in the Northern Hemisphere. *Proc. NIPR Symp. Polar Biol.*, **8**, 5–10.
- DROLET, R., FORTIER, L., PONTON, D. and GILBERT, M. (1991): Production of fish larvae and their prey in subarctic southeastern Hudson Bay. *Mar. Ecol. Prog. Ser.*, **77**, 105–118.
- FORTIER, M. (1994): Colonisation du lagon Saroma (Hokkaido, Japon) par les larves de poissons marins en relation avec la production de leurs proies zooplanctoniques sous le couvert de glace printanier. MSc Thesis, Université Laval, Québec, 60 p.
- FORTIER, L., PONTON, D. and GILBERT, M. (1995): The match/mismatch hypothesis and the feeding success of fish larvae in ice-covered Hudson Bay. *Mar. Ecol. Prog. Ser.* (in press).
- GILBERT, M., FORTIER, L., PONTON, D. and DROLET, R. (1992): Feeding ecology of marine fish larvae across the Great Whale River plume in seasonally ice-covered southeastern Hudson Bay. *Mar. Ecol. Prog. Ser.*, **84**, 19–30.
- HORNER, R. A. ed. (1985): *Sea Ice biota*, Boca Raton, CRC Press, 215 p.
- HORNER, R., ACKLEY, S. F., DIECKMANN, G. S., GULLIKSEN, B., HOSHIAI, T. *et al.* (1992): Ecology of sea ice biota 1. Habitat, terminology, and methodology. *Polar Biol.*, **12**, 417–427.
- KITAGAWA, D. and YAMASHITA, Y. (1986): Occurrence and distribution of the Japanese sand eel, *Ammodytes personatus*, larvae in the coastal waters of Iwate prefecture. *Bull. Jpn. Soc. Sci. Fish.* **50**, 205–213.
- LEGENDRE, L., ACKLEY, S. F., DIECKMANN, G. S., GULLIKSEN, B., HORNER, R. *et al.* (1992): Ecology of sea ice biota 2. Global significance. *Polar Biol.*, **12**, 429–444.
- RUNGE, J. A. and INGRAM, R. G. (1988): Underice grazing by planktonic, calanoid copepods in relation to a bloom of ice microalgae in southeastern Hudson Bay. *Limnol. Oceanogr.*, **33**, 280–286.
- RUNGE, J. A. and INGRAM, R. G. (1991): Under-ice feeding and diel migration by the planktonic copepods *Calanus glacialis* and *Pseudocalanus minutus* in relation to the ice algal production cycle in southeastern Hudson Bay. *Mar. Biol.*, **108**, 217–226.
- RUNGE, J. A., THERIAULT, J.-C., LEGENDRE, L., INGRAM, R.G. and DEMERS, S. (1991): Coupling between ice microalgal productivity and the pelagic, metazoan food web in southeastern Hudson Bay: A synthesis of results. *Polar Res.*, **10**, 325–338.
- TAGUCHI, S. and TAKAHASHI, M. (1993): Summary of the colloquium. *Bull. Plankton Soc. Jpn.*, **39**, 152–154.

(Received April 12, 1994; Revised manuscript received August 18, 1994)